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RESEARCH ARTICLE

The private life of echidnas: using accelerometry and GPS to examine field biomechanics and assess the ecological impact of a widespread, semi-fossorial monotreme

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ABSTRACT

The short-beaked echidna (*Tachyglossus aculeatus*) is a monotreme and therefore provides a unique combination of phylogenetic history, morphological differentiation and ecological specialisation for a mammal. The echidna has a unique appendicular skeleton, a highly specialised myrmecophagous lifestyle and a mode of locomotion that is neither typically mammalian nor reptilian, but has aspects of both lineages. We therefore were interested in the interactions of locomotor biomechanics, ecology and movements for wild, free-living short-beaked echidnas. To assess locomotion in its complex natural environment, we attached both GPS and accelerometer loggers to the back of echidnas in both spring and summer. We found that the locomotor biomechanics of echidnas is unique, with lower stride length and stride frequency than reported for similar-sized mammals. Speed modulation is primarily accomplished through changes in stride frequency, with a mean of 1.39 Hz and a maximum of 2.31 Hz. Daily activity period was linked to ambient air temperature, which restricted daytime activity during the hotter summer months. Echidnas had longer activity periods and longer digging bouts in spring compared with summer. In summer, echidnas had higher walking speeds than in spring, perhaps because of the shorter time suitable for activity. Echidnas spent, on average, 12% of their time digging, which indicates their potential to excavate up to 204 m^3 of soil a year. This information highlights the important contribution towards ecosystem health, via bioturbation, of this widespread Australian monotreme.

KEY WORDS: *Tachyglossus aculeatus*, GPS, Digging, Stride, Locomotion

INTRODUCTION

Echidnas are members of the family Tachyglossidae, a group of spiny, egg-laying mammals that inhabit Australia and New Guinea. The four extant species of echidna, together with the platypus, are the only surviving members of the order Monotremata, which diverged from the therian mammals (placentals and marsupials) around 166 million years ago (Bininda-Emonds et al., 2007). The biology of echidnas is therefore of particular interest, as representatives of this ancient mammalian lineage. The short-beaked echidna (*Tachyglossus aculeatus*) is the most-studied monotreme, because of its wide distribution throughout most Australian terrestrial environments. It is a medium-sized mammal (2–5 kg) covered on its back and sides with fur and stout spines (Augee et al., 2006). Its head is relatively small given its stocky body, and tapers to a long, hairless, cylindrical snout, which it uses to probe the ground in search of the ants and termites that comprise the greatest proportion of its diet (Griffiths, 1978).

The appendicular skeleton of monotremes differs considerably from that of therian mammals, with the retention of some ancestral reptilian characteristics (Jones, 1923). The combination of plesiomorphic and adaptive (apomorphic) characteristics influences the limb morphology of short-beaked echidnas, reflecting both their evolutionary history and modern digging habit. The monotreme coracoid process has a reptilian structure – it is large and fixes the shoulder to the axial skeleton by running from the shoulder joint to the sternum, compared with the small coracoid process on the scapula of therian mammals that does not reach the sternum. The pelvis retains epipubic bones (in common with marsupials, but lost in placental mammals). The limbs are short and stout and both the femur and humerus project horizontally, resulting in a sprawling but narrow posture that is well suited to excavating ants and termites (Nicol, 2015). The hind limbs are longer than the forelimbs and the tibia and fibula are rotated posteriorly so that the hind feet turn backwards (Griffiths, 1989).

The unusual morphology of the monotreme appendicular skeleton means that their biomechanics of locomotion are of particular interest. However, there are relatively few biomechanical studies of monotremes. Echidnas have a characteristic rolling gait, during which the trunk rolls and yaws, and there is no lateral undulation, as observed for reptiles (Nicol, 2015). Cineradiographic studies of limb bone kinematics for the short-beaked echidna (Jenkins, 1970, 1971) noted that the limb movements did not reflect the upright posture typically reported for cursorial mammals (Gray, 1944), nor the sprawling posture of lizards (Clemente et al., 2013), but rather was an intermediate locomotor mode between these groups. The closely related long-beaked echidna (*Zaglossus bruijni*; Gambaryan and Kuznetsov, 2013) has a similar gait as the short-beaked echidna, somewhere between slow/moderate, single-foot/lateral-couplets in terms of Hildebrand's nomenclature (Hildebrand, 1965, 1966, 1967, 1968) or a slow pace-like walk in terms of Sukhanov (1967, 1974), making it unusual for a mammal. Although echidnas use dynamic rather than static equilibrium when moving, they do not run and always have at least two points of contact with the ground, resulting in low maximum speeds of about 2–3 km h^{-1} (0.5–0.8 m s^{-1}; Nicol,

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2015). The energetics of walking by the short-beaked echidna (Edmeades and Baudinette, 1975) indicate a similar rate of increase in energy expenditure with speed as for other mammals (Taylor et al., 1974), but a lower absolute cost, probably as a result of its lower resting oxygen consumption. These findings for captive echidnas measured in the laboratory suggest that the locomotory mode of echidnas is distinct, and represents a unique combination of phylogenetic history and ecological specialisation to a semi-fossorial habit.

The short-beaked echidna forages by digging into ant and termite mounds, or underneath fallen wood and tree bases (Nicol, 2015). Diggings in ant mounds have been described as small round conical holes 25–80 mm deep made by the thrust of the snout, larger holes with a broader working face (conical in the first part and ending in a snout hole) and diggings in looser soil as shallow or deep excavations or extensive 'bull-dozing' tracts; they dig deep well-formed burrows with a flat floor and arched roof (Griffiths and Simpson, 1966; Rismiller, 1999, cited by Eldridge and Mensinga, 2007). In areas where this species is present, evidence of its digging is particularly abundant. These diggings may have substantial ecological importance as a source of soil bioturbation. Bioturbation is a mechanical form of ecosystem engineering that can alter soil physical and biotic properties (James et al., 2009; Reichman and Seabloom, 2002), resulting in increased soil mixing (Zhang et al., 2003) and species diversity (Ceballos et al., 1999; Davidson and Lightfoot, 2008). Although most mammals associated with bioturbation in Australia have suffered considerable reductions in density and distribution post-European settlement (Fleming et al., 2014; McKenzie et al., 2007) the short-beaked echidna is the Australian mammalian species least impacted; it has the widest geographical range of any Australian species and is listed as 'least concern' by the International Union for Conservation of Nature red list (Nicol, 2015). Therefore, it may be one of Australia's most important living bioturbators, yet the extent and time it spends digging has not been accurately recorded.

Accelerometers provide useful information concerning movement, to infer biomechanics and ecologically relevant movement patterns. The recording of acceleration using animal-borne electronic devices is gaining popularity (e.g. Brown et al., 2013; Martiskainen et al., 2009; Nathan et al., 2012; Shepard et al., 2008; Williams et al., 2016; Wilson et al., 2006). The measure of acceleration typically includes both static (due to gravity) and dynamic (due to movement) components, which are recorded whilst the animal carries out routine behaviours (Sato et al., 2003). Using accelerometers, biologists can quantify the movement and behaviour of wild animals during biologically and ecologically significant events and periods, unlimited by visibility, observer bias or geographic scale (Williams et al., 2016). For example, Lush et al. (2016) used accelerometry to classify various behaviours for free-ranging brown hares (*Lepus europaeus*). Accelerometers have also been used to record how hunting dynamics in cheetahs (*Acinonyx jubatus*) change while hunting different prey and the relative importance of speed versus turning ability (Wilson et al., 2013b). Accelerometers can also be used in combination with other sensors, such as those recording location, to provide a wide range of detailed information on the environmental context of animal behaviour that can exceed the descriptive abilities of a human observer (Williams et al., 2016; Wilson et al., 2013a). Accelerometers are therefore an ideal approach for examining the biomechanics of echidna locomotion and foraging, for a species that can be difficult to observe undisturbed in the wild, and for which captive conditions may impact behaviour and locomotory activities (Griffiths, 1989; Jones, 1923). Here, we use accelerometer data, combined with GPS tracking, for 11 echidnas in summer and spring 2012–2014 to examine the biomechanics of wild, free-living echidnas in a semi-arid open woodland habitat. We then apply these data to predict the impact that the echidna may have on Australian ecosystems in the form of bioturbation. We examine several aspects of echidna movement: (1) how does the biomechanics of echidnas compare to other mammals? (2) How far and how fast do echidnas walk during a typical day? (3) How long do echidnas spend foraging and digging each day? (4) Over what area does foraging occur? and (5) Do these patterns of movement change in different seasons? This information will help us to paint a picture of an echidna's daily life, which may be an important tool for environmental management and in estimating ecosystem health.

MATERIALS AND METHODS

Study animals and field site

Eleven adult echidnas [mean body mass (M_b)=3.23±0.02 kg] were studied at Dryandra Woodland (approximately 170 km South East of Perth, Western Australia 31° 46′ S 117° 1′ E). Two seasons of data were collected: summer, 1–11 February 2013 (n=5) and spring, 11–21 October 2014 (n=6). Echidnas were captured by hand and then fitted with accelerometers (see description below), GPS units (Cat Track 1, Catnip Technologies, Anderson, SC, USA, 1 fix per minute) and radio transmitters (RI-2C, Holohil, Ontario, Canada), by bundling these in tape and attaching them posterior-dorsally to an aluminium cradle glued with epoxy adhesive to the spines of the lower back.

Echidnas were located and recaptured with the aid of the radio transmitter every 1–4 days to download data from and recharge batteries of the accelerometers and GPS units, up to a maximum of 6 days per individual. Before capture and after release, movements were filmed using a high-speed hand-held camera (Casio EX-FH25, Casio, Japan) at 120 frames s^{-1}. In total, 64.5 min of echidna footage was collected of echidnas undertaking natural behaviours. Before each release, echidnas were hand held and filmed while they were moved in x, y and z planes to set the orientation of the accelerometer (Movie 1). Each individual was also filmed moving across flat open ground at various speeds alongside a tape measure; the camera (Pentax DSLR K50 in video mode; 29.97 frames s^{-1}) was held stationary, perpendicular to the direction of movement. At the conclusion of the study, transmitters and metal cradles were trimmed from the spines, and echidnas were released at the site of last capture.

All experiments were performed according to the Australian Code of Practice for the care and use of animals for scientific purposes, with approval from the Curtin University Animal Ethics Committee (AEC/2013/04, AEC/2014/04), inter-institutional approval by the University of Western Australia and University of Queensland animal ethics committees, and under licence from the Western Australian Department of Parks and Wildlife (SF009683).

Accelerometers

The accelerometer logging device used for the summer study comprised an 8-bit microcontroller (MSP430F2272) and a digital tri-axial accelerometer (LIS302DL) that was logged at 100 Hz with a dynamic range of ±2G at 8-bit resolution. Data were stored on a 2 GB micro-SD card. The device was powered by a 100 mAh lithium-ion battery regulated by a buck-boost switch-mode power supply (MAX1159). All electronics (except for the battery) were mounted on a circular printed circuit board with diameter 25 mm. The battery (25 mm in diameter; 4 mm width) was secured parallel to the board.

This design had substantial battery life limitations (typically achieving only 24 h logging time), but in the interim period between the summer and spring studies, a new logging device was

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developed. This device comprised a 32-bit micro-controller (PIC32MX695F512H) and a digital tri-axial accelerometer (MPU9150) that was logged at 10 Hz with dynamic range of ±4G and 16-bit resolution and data stored on an 8 GB micro-SD card. The device was powered by a 700 mAh lithium-ion battery regulated by a buck-boost switch-mode power supply (TPS63030). All electronics (except for the battery) were mounted on a square printed circuit board with 25×25 mm. The battery was secured parallel to the board, and protected with a conformal coating.

Biomechanical analysis

We used the serial digital pictures of each echidna as it moved alongside a tape measure over open ground at various speeds to determine stride length (SL), stride frequency (SF) and locomotor speed (v). The position of the head of the echidna was digitised in MATLAB (v.R2012a, MathWorks) using DLTdv3.m (Hedrick, 2008) and displacement data were smoothed using the smooth.m function, which performs a Robust Lowess (linear fit) over a 0.2 s moving time window. Each stride began at lift-off of the right hindlimb and ended with the subsequent lift-off of the same limb. Stride length was the linear movement distance of the hindfoot between footfalls, in metres. Stride frequency was 1/time between footfalls, in s^{-1}. The average speed over the stride (m s^{-1}) was determined using the mean of the instantaneous speeds for all frames between footfalls.

Activity analysis

Accelerometer data were analysed using a custom-written MatLab script (C.J.C. and P.T.). High-speed video and accelerometer traces were aligned using time stamps on both the film and accelerometer trace. Aligned video was assessed and manually characterised into one of four behaviours: inactivity, walking, digging/foraging and climbing over obstacles. Inactivity was characterised by no significant or coordinated x, y or z accelerometer signals (e.g. Fig. 1A). Walking was characterised by a high-frequency, high-

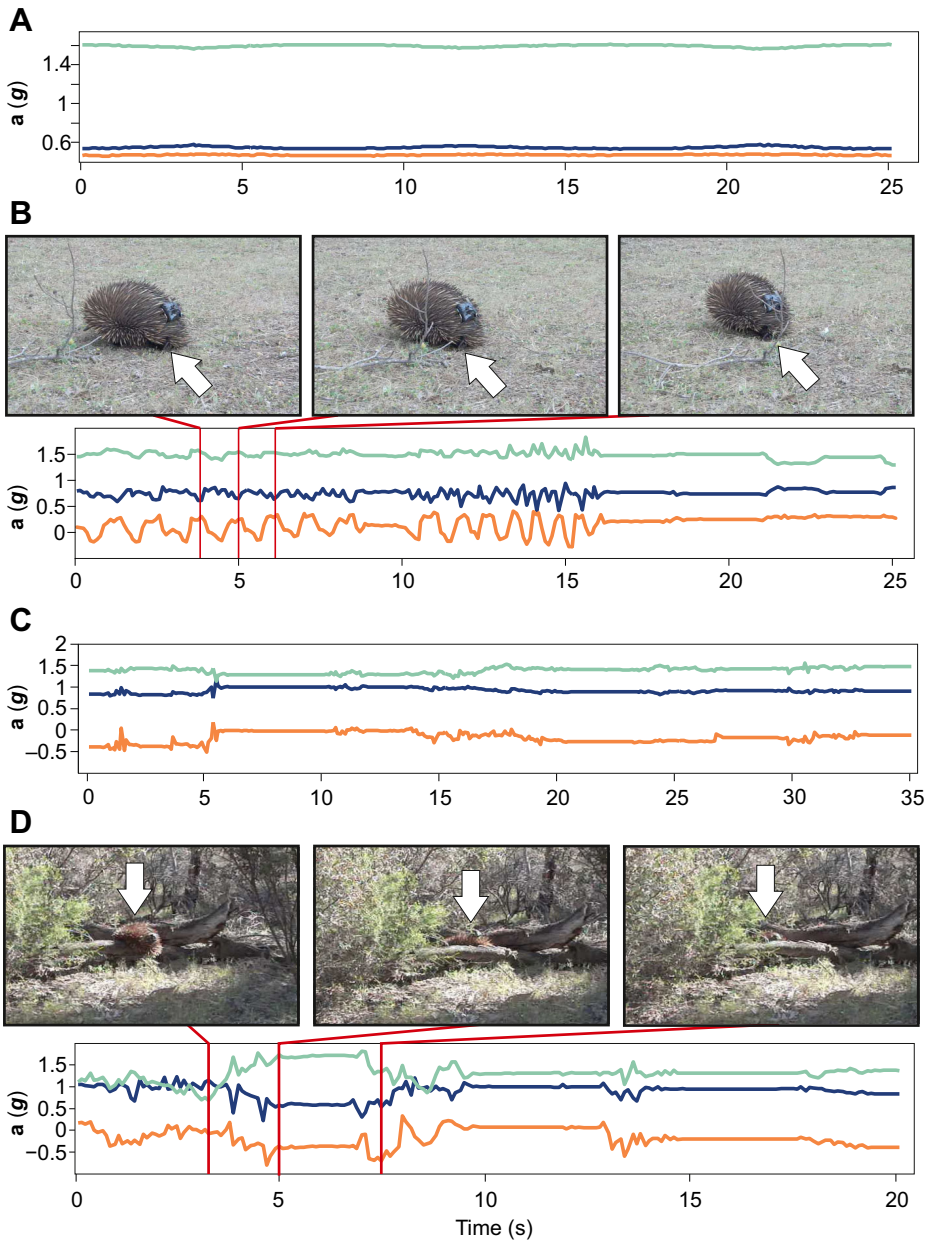

Fig. 1. Accelerometer traces showing activity of a short-beaked echidna. (A) Inactive, showing no variation of the accelerometer traces. (B) Walking, showing periodic fluctuations; each peak represents a complete stride cycle, indicated by the lift-off of the left hindlimb (arrow). (C) Digging, indicated by low amplitude, periodic sections of activity; (D) climbing, showing a shift in the baseline of the accelerometer. Colours represent accelerometer traces in x (dark blue), y (orange) and z directions (green). Arrows correspond to events indicated in red on traces below.

amplitude continuous movement (Fig. 1B; Movie 2) and digging/foraging by a low-amplitude, intermittent pattern of movement (Fig. 1C; Movie 3). Climbing was characterised by a distinct temporal shift in the baseline, indicating an ascending phase and a descending phase (Fig. 1D; Movie 4). Owing to the abrupt nature of the events, we interpret these climbing epochs as small log or other obstacle negotiation events, rather than extended incline or decline traversing events.

Accelerometer data for each recording were then imported into MatLab and as part of this process, summer studies were downsampled to 10 Hz to ensure consistency with the spring studies. A customised MatLab graphical user interface (Fig. S1) was used to segment the accelerometer data into discrete 30 s epochs. Using accelerometry segments associated with video activities as training data, each epoch was manually assigned to one of the four activities. All behaviours that could not be classified into one of these categories were marked as unknown. Data were then imported into R (v.3.0.2). We removed the first 20 min of activity immediately following release to remove any handling effect. To determine the accuracy and repeatability of the manually assigned behaviours, we characterised the accelerometer traces on a 30 s epoch-by-epoch basis using 10 relevant feature vectors (see Table S1 for full description) established by their use in previous accelerometer studies (Campbell et al., 2013). We then performed a linear discriminant function analysis, with jack-knifed (i.e. leave one out) predictions using the LDA.R function from the MASS package in R (Venables and Ripley, 2002). Before analysis, data were scaled and centred using the scale.R function from the base package in R. The accuracy of the feature vectors to predict the activity was assessed relative to the prediction.

Analysis of the aligned film also revealed that first peak frequency of the accelerometer trace coincided with a complete stride cycle (Fig. 1B; Movie 2). This suggests that the peak frequency of the accelerometer traces within walking epochs can be used to estimate stride frequency. To determine peak frequency, we calculated the power spectral density for the sum of all three axial accelerometer bands, for each 30 s walking epoch, using the function pwelch.m from the signal toolbox in MatLab (Fig. S2). We then searched for the peak frequency in the range 0.35–2.3 Hz (i.e. ignoring higher frequency 'harmonics') as this reflects the range of walking speeds observed for freely moving echidnas (see below).

Walking speed and walking distance were then calculated for each 30 s epoch. Walking speed was calculated from the relationship between stride frequency and speed (see below). Stride frequency was also used to estimate the number of steps taken in each epoch. Stride length was estimated from the relationship between stride frequency and stride length, and the product of stride length and the number of steps allowed an estimation of the distance travelled in each epoch. For each estimation, based on these biomechanical relationships, we performed an additional sensitivity analysis using the upper and lower 95% confidence bounds for each regression. We calculated the mean values of walking speed and walking distance for all epochs within each hour for each individual on each day, and used these values in a statistical analysis of our data.

GPS data

GPS data were also analysed for comparison with, and to contribute to, the accelerometer analysis above. We tested the accuracy of the GPS unit by walking south along a road in our field site, and compared the average GPS deviation from 'known' GPS co-ordinates retrieved from Google Earth; while moving, the average deviation for 11 GPS units was 5.37±0.90 m (mean±s.e.). GPS deviation increased to 21.79±8.71 m when the GPS unit was held stationary.

To remove this noise in our GPS data, we smoothed both the latitude and longitude data independently using Robust Lowess (linear fit) and used the smoothed coordinates to generate a likely path of travel for the echidna. For each GPS fix we then calculated the error in both the latitude and longitude data away from this likely path, and excluded any points that were greater than 1 standard deviation away from the path (Fig. 2A). The distance moved between fixes was determined using the Haversine prediction and the speed travelled between fixes was then estimated from the time difference. As for the accelerometer data, we calculated the mean values of speed and distance for all fixes within each hour for each individual on each day; these mean hourly values for each individual were used for statistical comparisons.

To calculate the minimum convex polygon area over which activity occurred we used the adehabitatHR package in R (Calenge, 2006). Latitude and longitude data were imported in decimal degrees and converted to a spatial class using the SpatialPoints.R function and assigned to WGS84 as the coordinate reference system using the proj4string.R function. These points were then transformed into the local UTM 50 s (epsg: 32750) reference system for Western Australia using the spTransform.R function. The minimum convex polygon area was then calculated using the mcp.R function excluding 5% of outliers (Fig. 2B). Values were calculated for each echidna and for each day for use in statistical analysis. Since our echidnas were primarily nocturnal, we separated our days at midday, so as to not subdivide the area moved throughout the nocturnal activity period.

Ambient temperature

Ambient temperature (T_a) was recorded during both spring and summer data collection periods. During the summer collection period we retrieved information from the Bureau of Meteorology data collection station in Wandering, WA (10917), located approximately 27.5 km North West of the centre of our field site. In spring, we used a calibrated temperature logger (±0.58°C, Thermochron iButton, Dallas, Texas), placed in the shade, in Dryandra Village, at the centre of our field site. For both datasets, we used the dry bulb temperature recorded each minute, and calculated the mean temperature, and the 75th and 25th percentiles, for each hour, over the entire sampling period.

RESULTS

Locomotor biomechanics

We quantified the walking speed, stride length and stride frequency of short-beaked echidnas based on 62 strides, from 17 sequences filmed from 5 echidnas in spring. Speed varied from 0.06 m s^{-1} to 0.65 m s^{-1} with an average speed of 0.31 m s^{-1}. Stride length varied from 0.09 m to 0.28 m, with an average of 0.20 m, whereas stride frequency varied from 0.35 Hz to 2.31 Hz, with a mean value of 1.39 Hz. Stride frequency (SF) was a better predictor of speed (v) than stride length (SL; Fig. 3) with regression relationships of v=0.278 SF–0.075 (R^2=0.92, $F_{1,60}$=747, P<0.001), compared with that of v=3.429SL–0.390 (R^2=0.70, $F_{1,60}$=144, P<0.001). Stride frequency was related to stride length as SF=−0.682+10.132SL (R^2=0.51, $F_{1,60}$=64, P<0.001).

Activity classification from accelerometry

In total, 24,507 summer epochs and 78,183 spring epochs were included in the accelerometry analyses. A linear discriminant analysis (LDA) including 10 accelerometer feature vectors (Table S1) was

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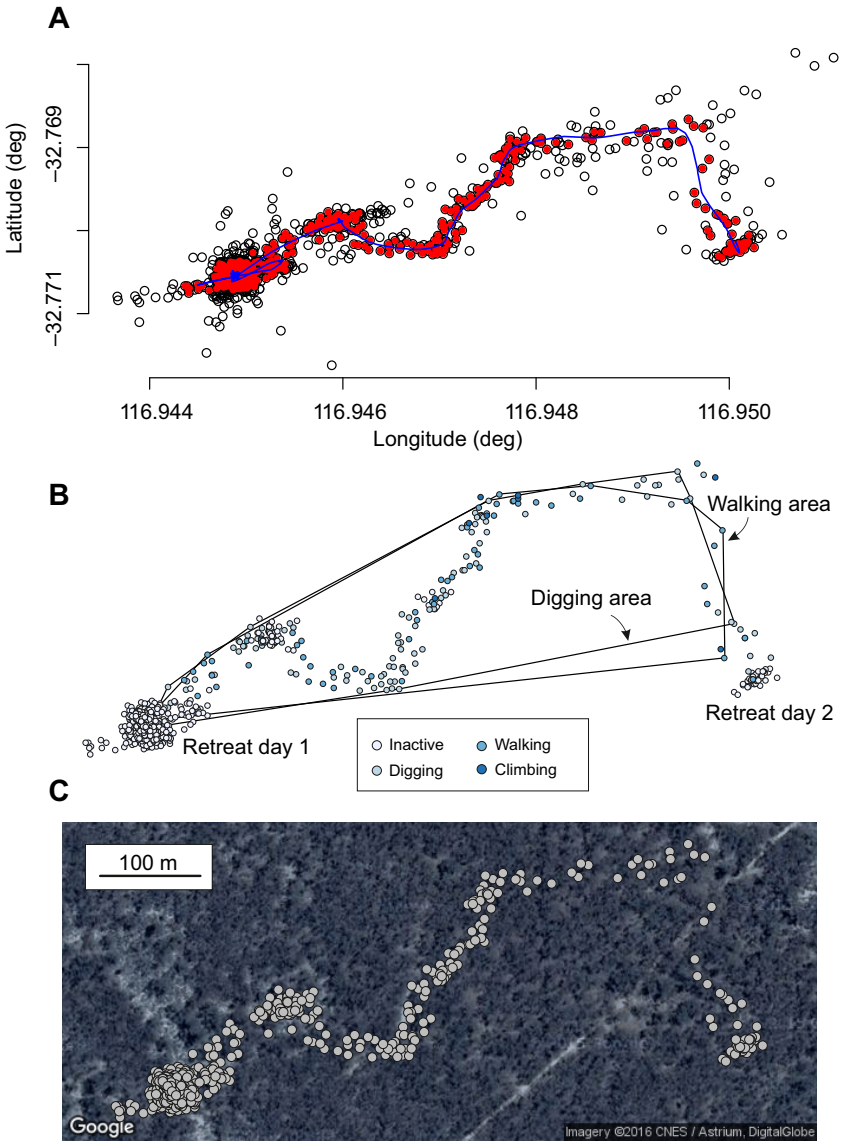

Fig. 2. GPS data for an active echidna during summer. (A) Example of smoothing process to remove noise. A line representing smoothed data via Lowess fit is shown in blue. GPS fixes within ±1 s.d. of this line are shaded red, and are included in further analysis. Open circles representing noise are excluded. (B) Combining activity determined using accelerometer data with GPS fix data to get daily walking and foraging area. Polygons represent foraging area estimated using the minimum convex polygon from the adehabitatHR package in R. (C) GPS track (red symbols from A) plotted over a Google Maps satellite image using the gmap.R function from the dismo package in R (v. 1.1-1, https://CRAN.R-project.org/package=dismo).

generally able to accurately predict inactivity, walking, foraging/digging and climbing activities from the accelerometry signals. The LDA predicted an overall accuracy for the known activity videos of 95.0% for summer data and 95.1% for spring data. The loadings for the LDA functions were similar between the seasons (Table S2). For both spring and summer, the simple moving average (SMA) function, representing the overall movement intensity across all three axis within the epoch, was most highly loaded and separated walking epochs from inactive and digging epochs (Fig. S3). The loadings for the second LDA function varied more between seasons. In summer, it was characterised by high loadings of the maximum magnitude of acceleration within the epoch (AccMagMax), the standard deviation of z-axis accelerometer (SD_z), the wavelength form (WL) and SMA. In spring, it was similarly characterised by SMA but also the standard

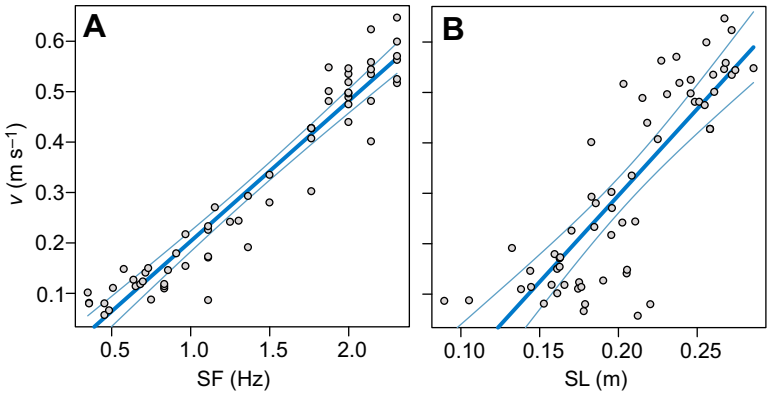

Fig. 3. Relationship of echidna locomotor parameters with speed. Speed as a function of (A) stride frequency and (B) stride length. Regression lines are shown in blue, with 95% confidence intervals. N=5, n=62.

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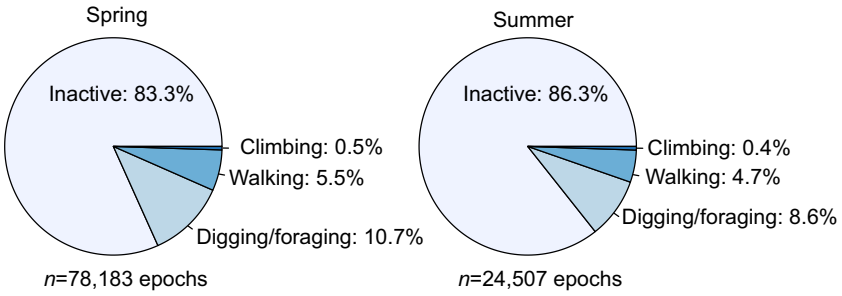

Fig. 4. Activity of echidnas in spring and summer. Data from echidnas in spring (left, *N*=6) and summer (right, *N*=5). Frequencies are based on assignment of 30 s epochs to one of the four identified activities: inactive, walking, digging/foraging and climbing.

deviation of *y*-axis accelerometer (SD_y). The second LDA function separated digging, from inactive and walking, for both seasons (Fig. S3).

The LDA results suggest that the most predictable activity pattern in both seasons was inactive, with 99.9% of known inactive epochs being accurately assigned in both the spring and summer datasets. Walking was the second best predicted activity, with 91.6% accurate assignment for spring data, and 91.2% accurate assignment for summer. Digging/foraging had a lower prediction accuracy, with 64.9% of epochs being correctly assigned for spring, and 53.8% for summer. Climbing activity was the most difficult to classify, with a 49.4% accuracy for spring data, but 60.2% accuracy for summer data.

Activities

The recorded epochs represented over 27.1 days (651.5 h) of activity from echidnas in spring and 8.51 days (204.2 h) from echidnas in summer. The activity durations of the echidnas did not vary significantly between the seasons, with a mean activity of echidnas in spring of 16.7±3.6% of time active per day, compared with summer 13.7±2.5% of time active per day (t_{11}=−1.07, P=0.307; Fig. 4). In both seasons, echidnas spent the majority of their time resting, usually in burrows, logs or caves. Echidnas spent much of their active time digging and foraging (10.7±2.2% of 16.7% of total daily activity in spring, 8.6±1.7% of 13.7% in summer), with the remainder of the time devoted to walking and climbing. Activities were not uniformly distributed throughout the

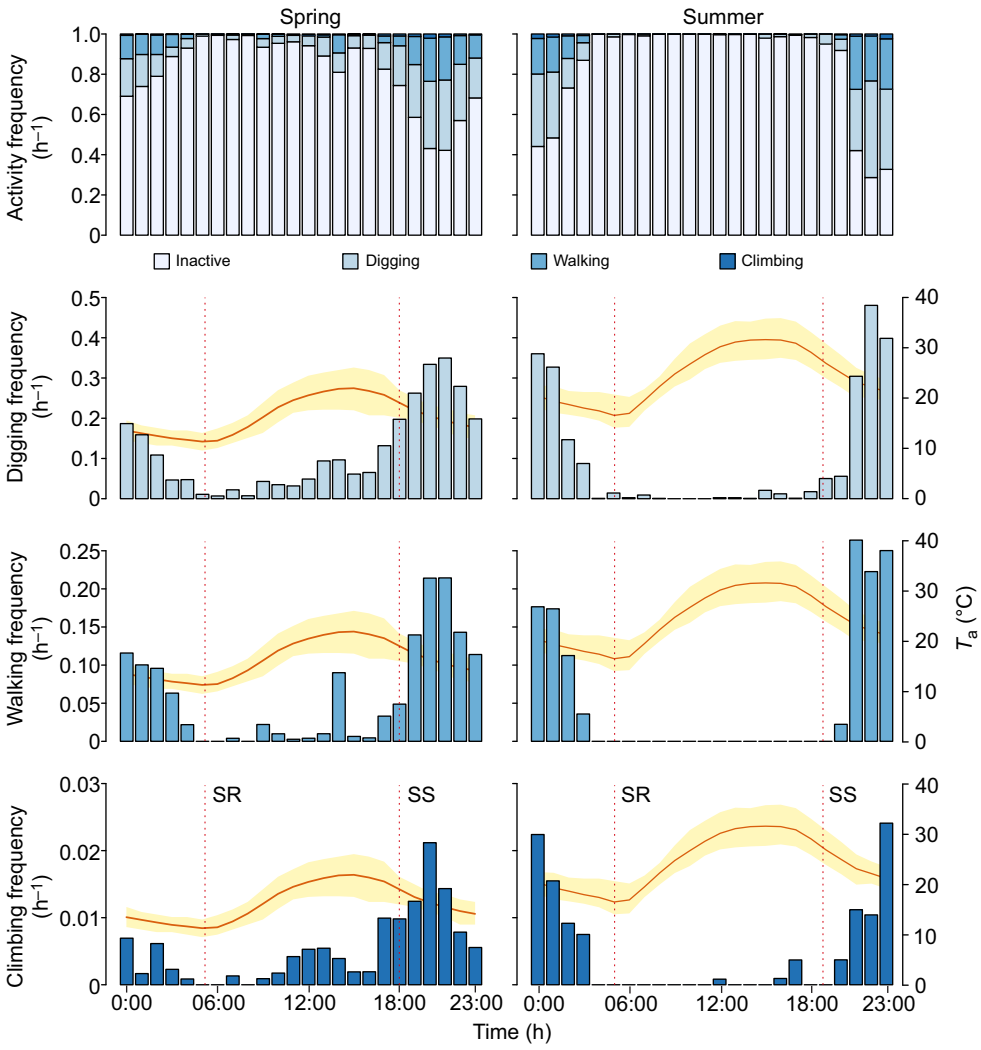

Fig. 5. Hourly activity frequency for each of the four activities. Spring activity is shown on the left (*N*=6, *n*=78,183), summer on the right (*N*=5, *n*=24,507). Mean ambient temperature in the shade is shown for each hour, with the lower and upper quartiles (yellow shading) indicating variation throughout the sampling period. Sun rise (SR) and sunset (SS) are indicated with dashed red lines.

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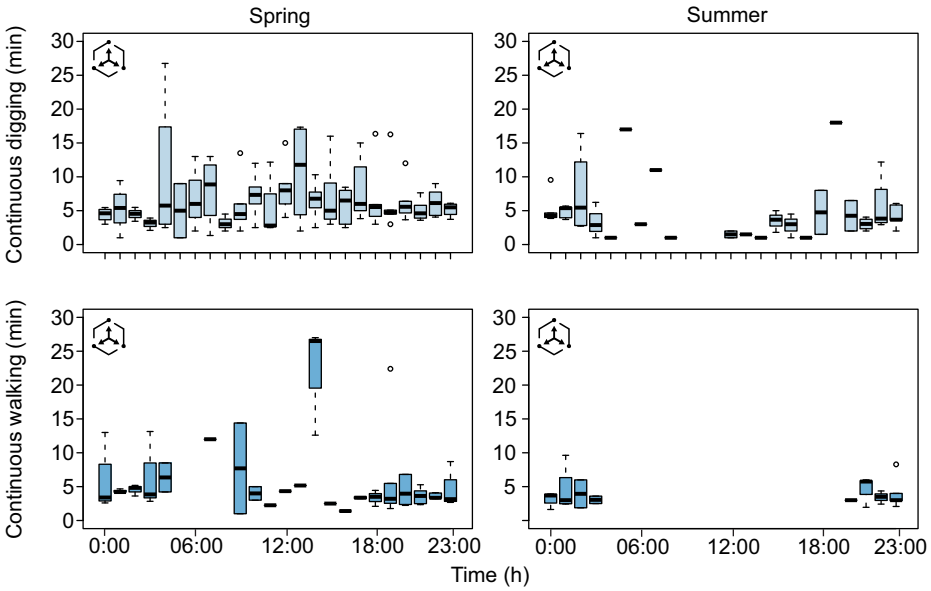

Fig. 6. Duration of activities of echidnas within each hour of the day. Data are shown for digging (top) and walking (bottom) for both spring (left) and summer (right), as determined by accelerometer. For each box plot the bold line indicates the 50th percentile of the data, while the lower and upper bounds of the box represent the 1st and 3rd quartiles, respectively. Whiskers represent the 1st and 3rd quartiles ±1.5 inter-quartile range, and circles represent outliers. Solid line only represents a single data point. Input data are mean per individual each hour; summer *N*=5, *n*=51 (digging), 25 (walking); spring *N*=6, *n*=106 (digging), 58 (walking).

day, but formed distinct daily patterns (Fig. 5). In spring, echidnas became active after 17:00 h, with a peak of activity for walking and climbing at 20:00 h shortly before a peak of digging activity at 21:00 h. Digging and foraging continued to taper off until 02:00 h, while walking and climbing continued a little past this time. In spring, echidnas had some low levels of activity throughout the day, especially in the early afternoon. In contrast, in summer, echidnas were almost completely nocturnal, with little or no activity during the day. Activity began at 19:00–20:00 h and rose sharply to peak between 22:00 h and 23:00 h before falling sharply again, dropping to zero around 03:00 h (Fig. 5).

We recorded 1477 individual walking bouts and 2060 digging bouts. The duration of digging but not walking bouts differed between the seasons. In summer, echidnas had shorter bouts of digging ($F_{1,132}$=5.82, P=0.017), although there was no significant seasonal difference for walking bout duration ($F_{1,61}$=1.76, P=0.189; Fig. 6). Average digging time for echidnas in spring was 6.49±0.41 min (n=106), while in summer, echidnas spent 4.73±0.56 min (n=51) digging at each foraging site. Walking times were similar, with a mean of 6.91±1.42 min in spring, whereas in summer, echidnas spent 3.92±0.41 min walking between foraging sites (Fig. 6).

We used this information, combined with power spectral density analysis of walking epochs (Fig. S2), to determine the likely walking speeds of, and distances travelled by, echidnas during their active periods. Walking speeds were higher for echidnas in summer [mean per hour per individual 0.399±0.013 (95% CI, 0.382–0.417) m s^{-1}, N=5, n=34] than in spring [mean per hour per individual 0.284±0.007 (95% CI, 0.267–0.301) m s^{-1}; N=6, n=108, t_{140}=7.65, P<0.001, Fig. 7A]. In spring, echidna walking speeds tended to peak early in the evening, around 17:00 h and again early in the morning around 04:00 h. For summer echidnas, variation in speed was less tightly associated with hour of the day, but maintained consistently high speeds, which were matched only in spring for short periods, at the start and end of each day's activity (Fig. 7A).

The distribution of speeds also varied between seasons (Fig. 8). Both seasons show that the preferred walking speed is between 0.25 and 0.35 m s^{-1}. However, during spring, echidnas use a greater proportion of slower speeds (0.05–0.25 m s^{-1}) and very few high-speed strides (0.5–0.65 m s^{-1}). In contrast, during summer, echidnas showed very few low-speed strides, but a greater proportion of high-speed strides. This probably explains their overall higher mean walking speed and may be linked to their shorter periods of activity during summer.

As for speed, the distance moved per hour was also higher for echidnas in summer (Fig. 7B): they moved an average of 321±34 (95% CI, 309–334) m h^{-1}, yet since they were only actively walking during 8 hours of the day, the total distance moved per day was 2575 (95% CI, 2477–2673) m. Echidnas moved significantly less per hour in spring (t_{27}=3.75, P<0.001), on average 168±22 (95% CI, 162–174) m h^{-1}, but they were active during 21 different hours of the day, meaning the sum total distance moved per day was estimated to be 3531 (95% CI, 3398–3662) m. Thus, in summer, echidnas appeared to move faster, but for a shorter period of time, therefore they covered less distance.

GPS data

In general, GPS data supported the accelerometer movement data (Fig. 7C,D). These data suggested that echidnas moved a mean distance in spring of 234±18 m h^{-1} (n=83), close to the mean distance estimate using accelerometer data of 168 m h^{-1}, although this predicts a higher summed daily distance moved of 5126 m because of the higher number of hours of activity per day compared with accelerometry data. For echidnas in summer, estimates of mean distance moved per hour were much lower using GPS data (73.13±7.78 m h^{-1}), and were significantly lower than for spring GPS estimates (t_{112}=8.09, P<0.001). This low estimate of mean distance moved per hour of activity for echidnas in summer also predicted a similarly low daily sum distance moved of 1654 m.

The mean speed estimate using GPS data was much lower than for accelerometer data, for both summer and spring data. Spring GPS data suggested an average movement speed of 0.089±0.007 m s^{-1}, while summer GPS data suggested a significantly lower mean speed of 0.04±0.02 m s^{-1} (t_{101}=8.72, P<0.001). The low speed estimates for echidnas in summer were at least partially due to GPS noise caused by estimating

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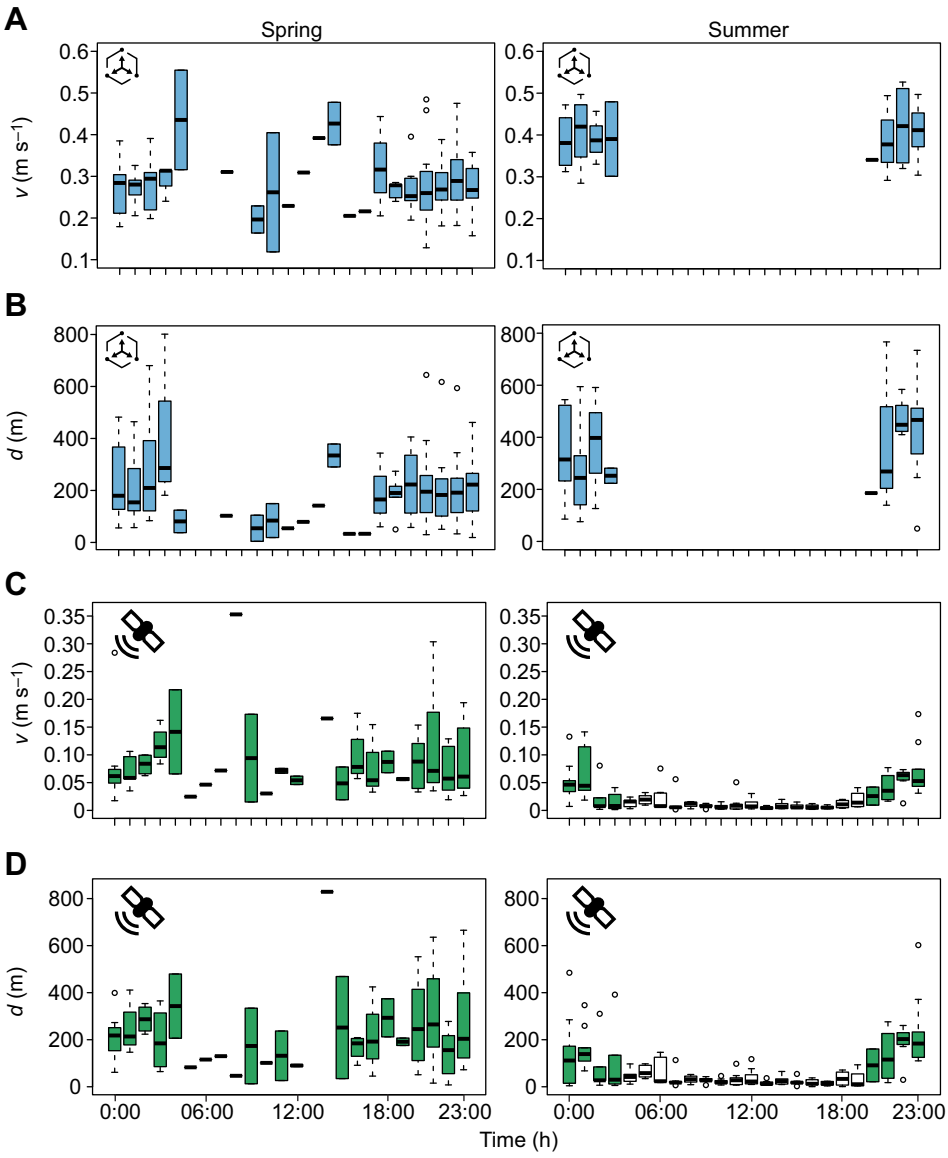

Fig. 7. Distance moved and walking speed of echidnas. Data are based on two different movement estimation methods; accelerometer data (A,B) and GPS data (C,D). Each hour is shown for spring (left) and summer (right). For accelerometer data, walking speeds were calculated from peak frequency from walking epochs input into stride frequency–speed regression analysis (Fig. 4). Distances moved were calculated from the product of the stride length–speed regression analysis and the estimated number of strides per epoch based on frequency (Fig. 4). For GPS data, shaded boxes indicate active periods estimated using accelerometer data. Non-zero estimates of distance and speed during non-active periods probably result from noise in GPS data. Box and whisker plots are as for Fig. 6. Input data are mean per individual each hour; summer N=5, n=34; spring N=6, n=108.

low speeds during hours when echidnas were known to be inactive (from accelerometer data). Excluding these inactive (accelerometer) hours resulted in a slightly higher GPS-estimated speed of 0.050±0.005 m s^{-1}.

The daily area over which activities occurred did not appear to vary strongly with season or with activity type. Including both season and activity type in an ANOVA when comparing the area bounded by a minimum convex polygon suggests no effect of activity ($F_{3,66}$=0.05, P=0.987, Fig. 2B), but a weak effect of season ($F_{1,66}$=4.268, P=0.043). This suggested that, in spring, echidnas tended to have larger areas of activity; however, this appears to be an effect of noise incurred during inactive periods. When we reduced our parameter space by excluding inactive and climbing activities, this second analysis showed no significant difference between the daily area over which walking and digging occurred ($F_{1,40}$=0.11, P=0.737) or any significant difference in the area of these activities between seasons ($F_{1,40}$=1.40, P=0.244). The mean daily foraging area (including both walking and digging) for spring echidnas was 41,521±8163 m^2 (41 ha), while the mean daily foraging area of summer echidnas was 29,925±4979 m^2 (30 ha).

DISCUSSION

The echidna provides a unique combination of phylogenetic history, morphological differentiation and ecological specialisation, and thus its biology is of particular scientific interest (Barker et al., 2016). This basal mammalian group has a unique appendicular skeleton and mode of locomotion, which are neither typically mammalian nor reptilian but retains aspects of both lineages (Nicol, 2015). We therefore were interested in the biomechanics of wild, free-living short-beaked echidnas to gain detailed information of their fundamental locomotory function in a natural environment, for comparison with other mammals. We then applied this basic information of echidna locomotory physiology in an ecological context, to better understand the ecosystem functions of echidnas in their natural habitat and their potential contribution to ecosystem health. This is of particular importance for echidnas as they are the most widely distributed terrestrial mammal in Australia and have not suffered the same significant declines in distribution and abundance as other native mammals (Nicol, 2015). They therefore have a considerable capacity to maintain their ecological role in a landscape where other bioturbators have declined or are extinct (Fleming et al., 2014).

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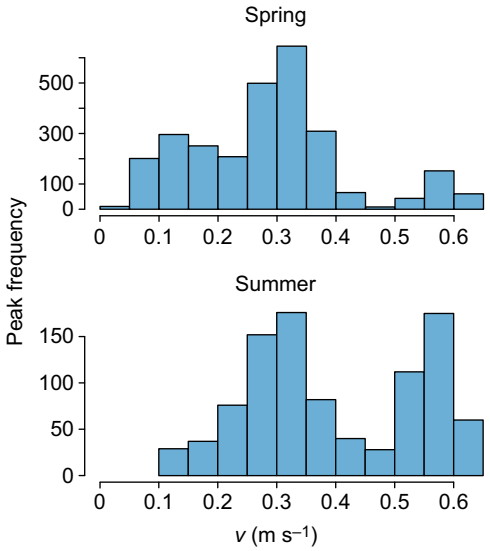

Fig. 8. Walking speed of echidnas in spring and summer. Walking speeds were based on accelerometer data, calculated from peak frequency from walking epochs input into stride frequency–speed regression analysis (see Fig. 6). Summer, *N*=5, *n*=967; spring, *N*=6, *n*=2752.

Biomechanics

The biomechanics of the short-beaked echidna in the field reflects that of the related long-beaked echidna (*Zaglossus bruijni*) determined from a single 7.3 kg captive specimen (Gambaryan and Kuznetsov, 2013). The average walking speed of the short-beaked echidna nearly exactly matches that reported for the long-beaked echidna (0.35 m s^{-1}), although the range of speeds reported here for short-beaked echidnas included a higher maximal speed of 0.65 m s^{-1}, which probably represents the top speed at which echidnas can move. The stride frequency reported here is over 1.7 times higher than that reported for the long-beaked echidna (Gambaryan and Kuznetsov, 2013). Yet, when compared with stride frequencies reported by Heglund and Taylor (1988), both echidna species have much lower stride frequencies compared with other similar-sized mammals (Fig. 9A) including the closely related 1.4 kg platypus (Fish et al., 2001). This is also the case for stride length; both the long- and short-beaked echidnas have relatively short strides, with the short-beaked echidna having the shortest, most constrained stride reported for any mammalian species (Fig. 9B). This is likely to reflect a restriction in the stride length resulting from a modification of the appendicular skeleton for a semi-fossorial, myrmecophagous lifestyle. The limbs of digging mammals, in contrast to the limbs of running mammals, have relatively shorter distal segments and this functional modification is also apparent for the short-beaked echidna (Casinos et al., 1993; Elissamburu and Vizcaíno, 2004; Hildebrand, 1985; Hildebrand and Goslow, 2001; Lehmann, 1963; Taylor, 1978). This configuration allows the limbs to produce the high force necessary to dig through the soil, although it necessarily reduces speed, largely through a reduction in stride length (Hildebrand, 1985; Hildebrand and Goslow, 2001). This interpretation is supported when considering the speed modulation strategies shown by these echidnas. The short-beaked echidna has a higher rate of change in stride frequency with speed when compared with the long-beaked echidna and other mammal species (Fig. 9C), suggesting a greater reliance on modification of stride frequency to increase speed. In contrast, the long-beaked echidna shows a greater modification in stride length with speed, reflecting its relatively longer limbs (Fig. 9D; Gambaryan and Kuznetsov, 2013).

Together, these results suggest that the locomotor ability of the short-beaked echidna is restricted, probably as a result of the structure of the appendicular skeleton. The effective predator defence afforded by the echidnas' dorsal spines has presumably allowed for a relaxed selection on locomotor speed, permitting modification of the axial skeleton to favour digging at the expense of velocity (Griffiths, 1989). Increased distal limb length and reduced bulk, favour longer, more rapid strides and faster running, but are at odds with the structural requirements for increased force generation needed for digging (Withers et al., 2016). For example, the forelimb structure of the fossorial eastern mole (*Scalopus aquaticus*) favours force generation to the detriment of rapid locomotion (Rose et al., 2013). Several other semi-fossorial

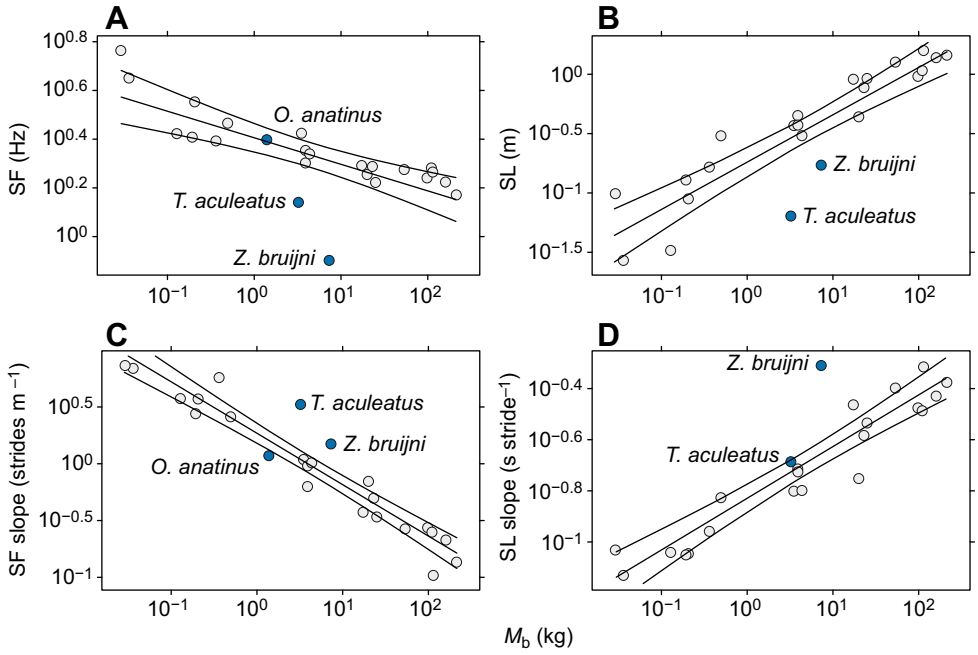

Fig. 9. Comparison of the stride characteristics from several mammal species. Data for the short-beaked echidna (*Tachyglossus aculeatus*) from Heglund and Taylor (1988) and Strang and Streudel (1990) (blue circles) is compared with that from this study (light grey circles), and with that for the long-beaked echidna (*Zaglossus bruijni*; Gambaryan and Kuznetsov, 2013) and platypus (*Ornithorhynchus anatinus*; Fish et al., 2001). (A) Stride frequency (SF) as a function of body mass, estimated from the slope and intercept of stride frequency with speed, at the mean speed from the speed range (Strang and Streudel, 1990). (B) Stride length (SL) as a function of body mass estimated from the slope of stride length with speed (Heglund and Taylor, 1988). Speed modulation strategies are also shown as the slope of stride frequency with speed, plotted against body mass (C) and the slope of stride length with speed, plotted against body mass (D). Regression lines and 95% confidence intervals for all data are shown.

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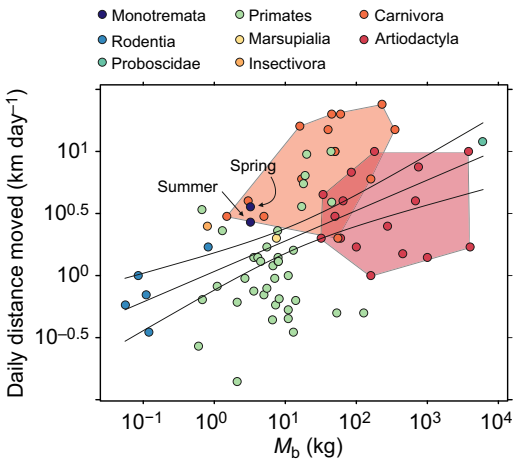

Fig. 10. Comparison of the daily distance moved with body mass for several orders of mammals and the short-beaked echidna. Data for mammals from Garland (1983) are based on radiotelemetric fixes, which may underestimate the daily distance moved. Data from echidnas are based on accelerometer data combined with our biomechanical analysis, with seasonal movement estimates included independently. The areas covered for Carnivora and Artiodactyla are shaded for clarity. Regression line and 95% confidence intervals are for all data compared with data for the short-beaked echidna (this study) (R^2=0.24).

myrmecophages, such as pangolins and armadillos, have also presumably traded off locomotor ability for digging and like the echidna, use armour to reduce susceptibility to predation (Lovegrove, 2001); moles and other truly fossorial mammals rely on their underground environment for protection. Put simply, you don't need to be able to run quickly if nothing can eat you.

Movement ecology

Short-beaked echidnas in our study were primarily nocturnal, with some diurnal activity bouts during cooler spring days. This is consistent with previous observations for echidnas obtained via radio telemetry, which indicate that ambient temperature has a significant influence on echidna activity, with predominantly nocturnal activity in warmer seasons and regions, and more diurnal behaviour in cooler seasons and habitats, such as alpine environments (Abensperg-Traun and De Boer, 1992; Augee et al., 1975; Brice et al., 2002; Grigg et al., 1992). As a consequence, echidnas during summer are much more constrained in their activity, with activity occurring in only 8 of 24 hourly blocks within a day compared with echidnas in spring that have some bouts of activity in 21 of the 24 hourly blocks within a day.

Echidna activity probably reflects seasonal variation in behaviour as a consequence of prey availability and also seasonal differences in energy requirements because of thermoregulatory and reproductive costs. Termites are the predominant prey of echidnas in the Western Australian wheatbelt region (Abensperg-Traun, 1988) and are found closer to the soil surface for short periods during cooler times of the day in summer, retreating deeper underground when the surface soil heats up. During cooler seasons, termites are more active close to the soil surface during the day when it is warmer (Abensperg-Traun and Boer, 1990). In addition, increased thermoregulatory costs during cooler periods, and seasonal fattening, possibly to support costs of late spring reproduction, presumably also contribute to the observed seasonal variation in activity (Abensperg-Traun and De Boer, 1992).

Despite the short periods of activity, or perhaps because of it, echidnas in summer must increase the pace of their foraging activity to make better use of the reduced available activity time. During summer, the walking speeds of echidnas were higher than during spring (Fig. 7A) as a result of a greater proportion of fast-paced strides close to the maximum speeds recorded (Fig. 8). The timing of these fast walking speeds indicates that echidnas emerge from their retreat (hollow log, rock cave or burrow) and move directly and rapidly to foraging sites. Once at these foraging sites, echidnas in summer undertook shorter bouts of digging compared with echidnas observed during spring (Fig. 6), which again supports previous reports obtained by radiotelemetry, of more extended, vigorous foraging in spring (Abensperg-Traun and De Boer, 1992; Augee et al., 2006). Short active periods have been reported for other nocturnal myrmecophagous species. For example, the Sunda pangolin (*Manis javanica*) is active for only 127±13 min day^{-1} (Lim and Ng, 2008). Camera trap data suggest that the giant anteater (*Myrmecophaga tridactyla*) is active during only 7 h of the day, less than for other mammals from a similar location (rodents, lagomorphs, ungulates and carnivores; Blake et al., 2012). These short active periods presumably relate to the low-energy lifestyle of myrmecophagous mammals (Cooper and Withers, 2002; McNab, 1984).

The total distance moved for echidnas was between 3.6 km day^{-1} (spring) and 2.7 km day^{-1} (summer). A comparison with other mammalian species (based on radiotelemetric fixes) suggests this daily distance moved is somewhat higher than for similarly sized mammals (Fig. 10) and more closely reflects that of carnivores, which have been suggested to move about 4.4 times greater distances than other mammals (Garland, 1983). This relatively high daily distance moved could reflect their low absolute cost of transport (despite the apparent inefficiency of echidna locomotion; Edmeades and Baudinette, 1975), low energy density of prey (Abensperg-Traun and Boer, 1990; Redford and Dorea, 1984) or a relaxed predation pressure, resulting from their extensive dorsal armament (Lovegrove, 2001).

Despite differences in movement patterns and distance moved between the seasons, the area over which echidnas foraged was similar in both spring (0.042 km^2 day^{-1}) and summer (0.030 km^2 day^{-1}). This suggests that the area required for sufficient foraging may be independent of season and the time available, but probably forces moderation of walking speed. Estimates of the short-beaked echidna's home range across Australia are between 0.4 to 1.1 km^2 (Augee et al., 2006; Nicol, 2015) and are 0.65 km^2 for wheatbelt reserves in Western Australia (Abensperg-Traun, 1991). Therefore, echidnas use ∼6.5% of their home range each day during spring and 5.0% during summer. As seasonal activity appears to be at least partly relate to ambient temperature, either directly or by indirectly impacting on prey activity and location, it is possible that increasing T_a within the south-west of Western Australia associated with climate change (Indian Ocean Climate Initiative, 2002) may alter the extent and duration of echidna activity and may reduce their role as ecosystem engineers, through bioturbation.

Digging ecology

The locomotor ecology of echidnas is not only of interest in an evolutionary and adaptive context, but it also impacts their potentially significant ecological role in contributing to ecosystem health (Eldridge and Mensinga, 2007). The potential ecosystem benefits for echidna diggings have been examined in eastern Australia's semi-arid eucalypt woodlands. The foraging pits

produced by echidnas almost double the amount of water absorbed (measured via sorptivity and steady-state infiltration) compared with undisturbed soils (Eldridge and Mensinga, 2007). Echidna diggings also increase soil heterogeneity, by capturing and retaining seeds and leaf litter, resulting in nearly twice the amount of organic debris as equivalently sized undisturbed areas (Eldridge and Mensinga, 2007). Furthermore, echidnas may contribute even more directly to ecosystem health, because mechanical turnover of the soil helps to trap organic matter below the surface (Fleming et al., 2014). This brings organic material into contact with soil invertebrates and microbes, which enhances the release of nutrients and nutrient cycling (James et al., 2010). For example, the soil respiration rate within echidna diggings was 30% higher than for nearby undisturbed soil (Eldridge and Mensinga, 2007). Yet, while bioturbation of the soil by echidnas has been demonstrated to improve ecosystem health, the extent and volume magnitude of this action is unclear.

Our study suggests that echidnas may make a substantial contribution to ecosystem health via soil bioturbation. We have established that echidnas spend up to 12% of their day digging. To roughly estimate the amount of soil turnover this could represent, we determined, based on video evidence, that echidnas were able to completely bury themselves in soil and leaf litter, within a minute. At this digging rate, echidnas could displace, each 30 s digging epoch, a half their body volume as dirt and leaf litter. We calculate the volume of an echidna based on a mean density of 1 g cm^{-3} (Mendez and Keys, 1960) to be 3230 cm^3 for a 3.23 kg echidna. Digging for 12% of the day means each echidna could move up to 0.558 m^3 of soil and leaf litter a day. Our seasonal data seems to suggest that this rate may be fairly consistent year round, which indicates the potential for each echidna alone, to move up to 204 m^3 of soil a year. This means that about 12 echidnas could move an amount of soil equal to the volume of an Olympic-sized swimming pool each year. Given the high population and wide distribution of echidnas in Australia, this species is likely a keystone species contributing to ecosystem health in Australia (Paine, 1995), especially considering the widespread decline and extinction of other potential mammalian ecosystem engineers.

Comparisons of accelerometer and GPS estimates

Previous studies of echidna activity and movement have relied on radio-tracking data (e.g. Abensperg-Traun, 1991; Augee et al., 2006; Brice et al., 2002), which can provide a coarse-scale picture of activity but cannot provide the fine detail of activity that we were able to record here. We also found that individual echidnas would learn to modify their behaviour over time to avoid our approach (by quickly retreating into hollow logs or rock caves), which could impact on the utility of direct observations of activity. To accurately measure biomechanics and movement ecology of echidnas on a fine scale, we used a combination of accelerometer and GPS units. This combination has been used previously (Bidder et al., 2015) and can offer a unique perspective on animal movement. Each measurement method has potential advantages and disadvantages, as our study has demonstrated.

Accelerometers are capable of rapidly and accurately measuring complex movements, and with a combination of biomechanical measurements we could infer speed and distance moved, at least within walking epochs. This technique did not, however, predict any movement during epochs assigned to digging since the peak frequency in these periods would be complicated by the additional action of bioturbation. This ability to differentiate activity appears to account for much of the variation between accelerometer-based estimates when compared with GPS-based estimates. Movement speed was lower for GPS-based estimates, since it includes epochs of inactivity and digging, which have relatively low walking speeds, driving overall mean estimates much lower. This suggests a limited ability for GPS measurements alone to resolve fine-scale estimates of walking speed.

Comparison of distance moved between the methods was much more complicated. GPS-based estimates of distance moved were higher for echidnas in spring but much lower in summer. This comparison is complicated by the multiple potential sources of measurement error associated with each technique. Distance moved could only be estimated during walking epochs for accelerometer data, which may exclude some smaller distances moved during foraging or climbing epochs, resulting in lower estimates for accelerometer-based techniques. Conversely, the accuracy of predicted GPS location becomes reduced when the animal is stationary, or deep in rock caves for long periods of time (D'Eon et al., 2002; Dussault et al., 1999; Frair et al., 2004; Gamo et al., 2000), meaning that the GPS output from a motionless echidna involved considerable scatter around a central point (Fig. 2A). This noise in the GPS signal results in non-zero estimates of distance moved when an animal is actually stationary (Fig. 7C,D). This could have the effect of increasing mean foraging distance estimates during inactive periods and may result in a higher overall estimate of mean distance moved, for example, as seen for echidnas in spring. GPS estimates must also assume a straight line travel between successive positions that does not often reflect the fine-scale movement patterns of a foraging animal (Kramer and McLaughlin, 2001). This could lead to an underestimation of distance moved, for example, as seen for echidnas in summer. While neither technique can provide error-free estimates of distance moved, both are probably useful for setting the upper and lower confidence bounds for fine-scale daily movement of animals.

Finally, since GPS data allow for the geographic location to be well defined, the area over which an animal foraged can be estimated; this information is not available from accelerometers. This is important when combining movement data with geographical features of the landscape in GIS programs (Fig. 2C). Thus, the combination of both GPS and accelerometer units can provide a detailed representation of the movements of an animal throughout the day.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization, C.J.C., P.C.W. and C.E.C.; Methodology, all authors; Software, C.J.C. and P.T.; Formal Analysis, C.J.C., P.C.W. and P.T.; Investigation, C.J.C., P.C.W., C.E.C. and C.F.; Writing – Original Draft, C.J.C., P.C.W. and C.E.C.; Writing – Review & Editing, C.J.C., P.C.W., C.E.C., P.T., S.S. and C.F.; Funding Acquisition, C.J.C, P.C.W. and P.T; Resources, P.T, S.S. and C.F.

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Data availability

Movies are available on Imgur: Movie 1, http://imgur.com/CsMJJKf; Movie 2, http://imgur.com/oAUr9gY; Movie 3, http://imgur.com/99JLPNX; Movie 4, http://imgur.com/cZKvjmM.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.143867.supplemental

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